FLOWER LONGEVITY AND PROTANDRY IN TWO SPECIES OF *GENTIANA* (GENTIANACEAE)[1]

C. J. WEBB AND JAN LITTLETON[2]

ABSTRACT

Both *Gentiana saxosa* and *G. serotina* are protandrous. When flowers open, pollen is presented extrorsely around the closed stigma for one to six days. As the stigma opens, the stamens curve toward the corolla lobes. The length of the female phase, and therefore reproductive flower life, is determined by pollination, although in both species the corolla may remain fresh for longer than one month. Fresh female-phase flowers close at night and fail to reopen on the day following pollination. After five days in the female phase, flowers reacted less quickly to pollination and seed production was reduced; flowers pollinated on their tenth day of stigma presentation produced no seed although they appeared fresh. Senescence of unpollinated flowers differed between species: in *G. saxosa* the flowers remained open and gradually deteriorated, but in *G. serotina* the flowers eventually closed before full senescence. Pollination-induced flower senescence has been demonstrated for a number of other angiosperms, and the usual reactions to pollination are corolla abscission, color change, or wilting. In *Gentiana*, the closed corolla enfolds the large superior ovary and may serve to protect it from predators as well as prevent further pollinator visits. Pollination-induced flower senescence probably also minimizes flower maintenance costs by ensuring that the flower functions no longer than necessary. One correlate of this phenomenon in hermaphroditic flowers is protandry, which ensures pollen dispatch before flower closure.

Floral senescence may be either time-dependent (endogenous) or exogenous (usually pollination-induced). However, there have been few detailed investigations of the factors that determine floral senescence, and hence, floral longevity (Primack, 1985). Most such studies have concentrated on corolla color changes or other physiological reactions that follow pollination and signal senescence (e.g., Arditti et al., 1973; Arditti, 1976; Gottsberger, 1971; Gori, 1983; Strauss & Arditti, 1984; Casper & La Pine, 1984; Halevy, 1984), and less attention has been afforded structural changes such as wilting, flower closure, and corolla abscission (Mayak & Halevy, 1980). Most of this research is concerned with the proximate determinants of floral longevity rather than the evolution of particular responses (but see Stead & Moore, 1979; Gori, 1983; Casper & La Pine, 1984; Devlin & Stephenson, 1984). The paucity of research on the evolutionary aspect of flower senescence is somewhat surprising, because pollination-induced senescence in particular may have important consequences for the pollination system and ultimately for the plant's overall reproductive strategy. For instance, in hermaphrodite flowers pollination-induced flower senescence will limit the duration of pollen and stigma presentation and so may influence or be influenced by the extent and nature of dichogamy (Lloyd & Webb, 1986).

New Zealand species of *Gentiana* (in the southern group of Philipson, 1972) are protandrous (Thomson, 1881; Simpson & Webb, 1980; Webb, 1984a). Their large, relatively simple flowers make them particularly suitable subjects for experimental studies of flower function. This paper describes the response of flowers of two species to pollination and reports the results of experiments to determine the functional duration of male and female phases in terms of pollen presentation and seed production.

MATERIALS AND METHODS

The two species of *Gentiana* selected were those that grew best in cultivation. *Gentiana saxosa* Forster f. grows naturally in coastal sites of southern South Island and Stewart Island, New Zealand; plants were collected from Curio Bay, Southland. *Gentiana serotina* Cockayne occurs in grassland in inland central South Island; plants were collected from Lake Lyndon, Canterbury. The plants were grown in clay pots in an insect-proof cage in greenhouses at Lincoln, Canter-

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[2] Botany Division, Department of Scientific and Industrial Research, Private Bag, Christchurch, New Zealand.

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TABLE 1. Results of controlled pollinations to determine self-compatibility in *Gentiana saxosa* and *G. serotina*.

	Treatment	Number of Flowers	Capsules Produced	% Seeds Produced per Capsule
G. saxosa	Cross-pollinated	10	10	94.2
	Self-pollinated	10	10	94.2
	Unpollinated	10	0	–
G. serotina	Cross-pollinated	5	5	57.9
	Self-pollinated	5	5	67.6
	Unpollinated	5	0	–

bury. Field observations were made at Lake Lyndon.

To test for self-incompatibility and autogamy 10 flowers in *G. saxosa* and five flowers in *G. serotina* were assigned to each of three treatments: self- and cross-pollination by hand, and unpollinated (Table 1). Flowers were tagged individually and observed daily. When capsules matured, they were harvested and good seeds and aborted seeds or undeveloped ovules were counted.

The duration of male and female phases was determined for individual tagged flowers. Pollen and stigma presentation were observed daily until petals withered and turned brown. Of 61 flowers of *G. saxosa* observed daily, five were cross-pollinated on each of the first to tenth days of their female phase, and 11 left unpollinated. Of 34 flowers of *G. serotina*, eight were pollinated on each of the first, fifth, and eighth days of their female phase, five on the tenth day, and five flowers were left unpollinated. For *G. serotina*, three flowers from each of the first, fifth, and eighth day pollinations were collected two days after pollination, the stigma dissected out, fixed, stained with aniline blue, and examined under fluorescent microscopy to determine the extent of pollen germination and pollen tube growth. For the remaining flowers, the responsiveness of each to pollination was quantified as the number of days until (a) the flower closed completely, (b) closed to its greatest extent (for flowers that closed incompletely), or (c) the number of days until the corolla withered and turned brown (for flowers that never closed). When capsules were mature they were harvested and seed production scored.

At Lake Lyndon, 10 fresh, unbagged, female-phase flowers of *G. serotina* were cross-pollinated by hand, and ten were left unpollinated. These flowers were examined the following day.

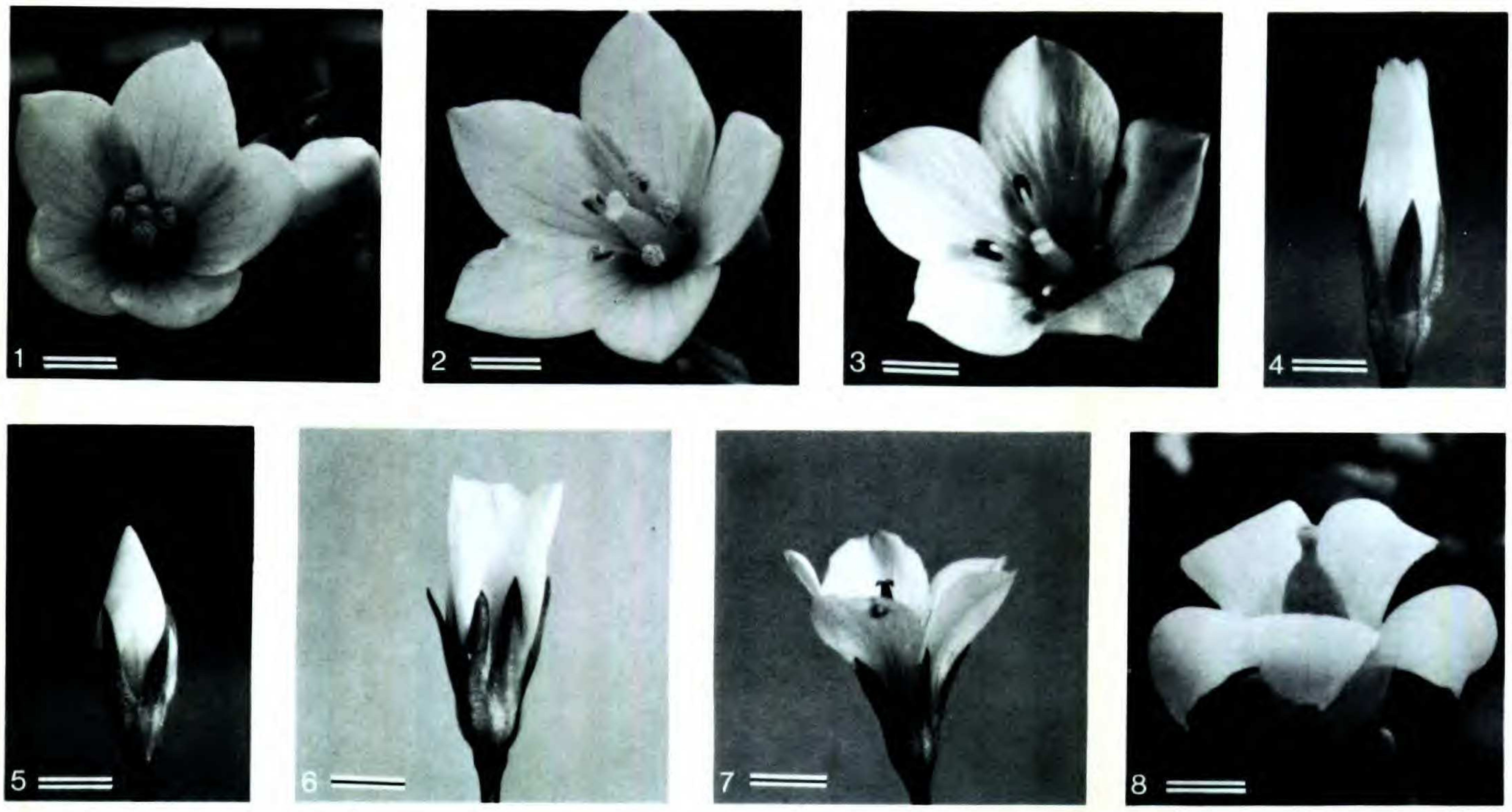
RESULTS

Flower form, phenology, and pollination. Both *Gentiana saxosa* and *G. serotina* are perennial herbs with a central leafy rosette and stout taproot. The flowers are on annual, leafy, lateral flowering branches that bear from one to eight flowers in *G. serotina* and one to 30 or more in *G. saxosa*. The corolla is deeply 5-lobed, white with translucent stripes on the lobes and upper tube (Fig. 1), and greenish-yellow toward the base of the tube. The five stamens are attached to the corolla tube; the anthers are purple and the pollen is cream to brownish-yellow. Nectar is produced between the bases of the filaments near the base of the tube. The central ovary contains an average of 29 ovules in *G. saxosa* and 47 in *G. serotina* (Webb, 1984a). The flowers lack a well-defined style; the stigma is 2-lobed, distinctly papillate, and dry.

In the field, *G. saxosa* blooms in summer and autumn (January to May), and *G. serotina* from late summer to autumn (February to May). Under greenhouse conditions *G. saxosa* reached peak flowering in December and *G. serotina* in March. The flowers are sweetly scented and visited on fine days by a range of insects. At Lake Lyndon, *G. serotina* was most frequently visited by syrphid flies and solitary bees (*Lasioglossum sordidum*). During anthesis, flowers opened completely only on fine days, and almost completely closed at night. On wet or cold, dull days few new flowers opened, and in those that had opened previously the corolla lobes did not spread completely.

Both *G. saxosa* and *G. serotina* are self-compatible (Table 1); however, flowers that were not pollinated and from which insects had been excluded failed to produce any seed, so biotic pollination is necessary for seed set.

Protandry. The flowers of both species are distinctly protandrous. In neither was there any obvious synchrony of male and female phases among flowers within a plant or even a flowering branch, so that within large plants pollen and



FIGURES 1–8.—1–7. Protandry and reaction to pollination in flowers of *Gentiana serotina* (bars = 0.5 cm).—1. First day open, male phase.—2. Fourth day, stigma opening.—3. Seventh day, stigma open, anthers near corolla.—4. Flower closing, one day after pollination of fresh female-phase flower.—5. Flower closed, two days after pollination of fresh female-phase flower.—6. Flower incompletely closed, five days after pollination on eighth day of female phase.—7. Unpollinated flower, 18 days.—8. Unpollinated flower of *G. saxosa,* 30 days (bar = 0.5 cm).

stigmas were presented simultaneously in different flowers and geitenogamy could occur.

When a flower first opens, the anthers have already dehisced to present pollen extrorsely near the center of the flower and the stigmatic lobes are tightly closed (Fig. 1). Later in the male phase, the corolla lobes open further, the stigma begins to open, and the stamens move outwards toward the corolla (Fig. 2). In *G. saxosa,* the stigma may open and stamens recurve late on the first day of anthesis, or as late as the fifth day. The mean duration of the male phase is 1.41 days (N = 57). In *G. serotina,* the stigma opens and stamens recurve between the third and seventh days (mean =4.73 days, N = 30). In *G. saxosa,* anthers have usually moved halfway toward the corolla when the stigma opens and have reached the corolla lobes in up to three days after that. In *G. serotina,* the anthers reach the petals and usually wither one or two days after the stigma opens (Fig. 3), and in some cases they eventually protrude between the corolla lobes. Although pollen is no longer presented in a central position by the time the stigma opens, there may be some overlap between pollen and stigma presentation within the flower, especially in *G. saxosa,* for which the male phase is shorter. However, under field conditions, little pollen usually remains by the time the stigma opens.

When the stigma opens the two lobes occupy the position in which pollen was presented in the newly opened flower (Figs. 1, 3). The duration of the female phase is dependent on pollination.

Reaction of the flower to pollination. Both species showed similar reactions to pollination. When fresh, first-day, female-phase flowers were pollinated, they partially closed that night and failed to reopen the following day (Fig. 4). Two days following pollination the corolla lobes were imbricate to form a neat, tight structure similar to, but slightly larger than a late bud (Fig. 5). The petals slowly turned brown and withered as the capsule reached maturity after about four weeks.

When the flower was pollinated on the second to fifth days of the female phase, the corolla reacted as quickly and folded as neatly as it did following first-day pollination. After the fifth day, although the flowers and their stigmas still appeared fresh, they reacted more slowly following pollination (Fig. 9), either taking several days to close or closing incompletely (Fig. 6). About one-third of the flowers pollinated after the fifth day of their female phase never closed completely. There was some variation among flowers of the

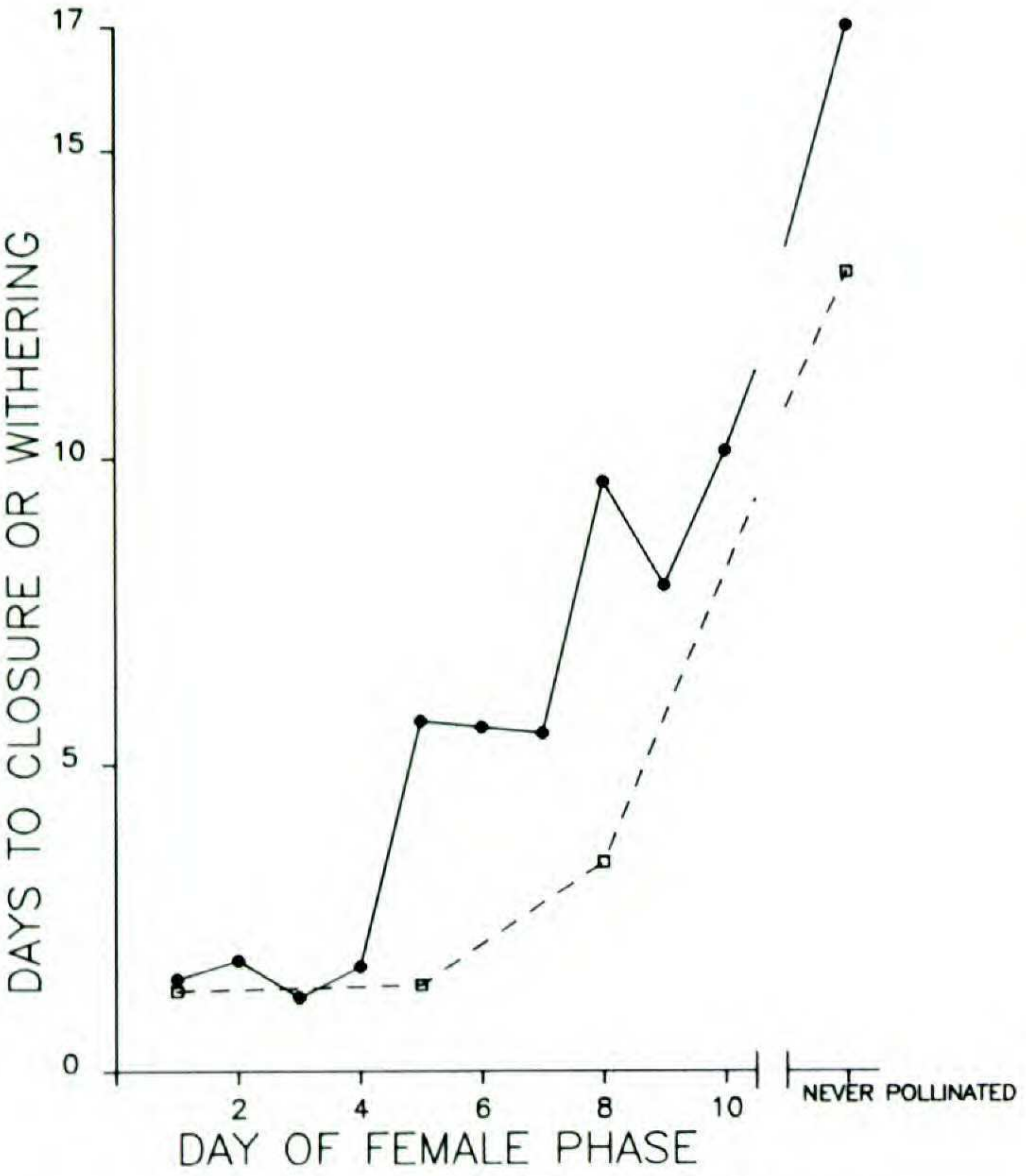


FIGURE 9. Days taken for flowers of *Gentiana saxosa* (solid dots) and *G. serotina* (open squares) to close or wither following pollination on different days of female phase.

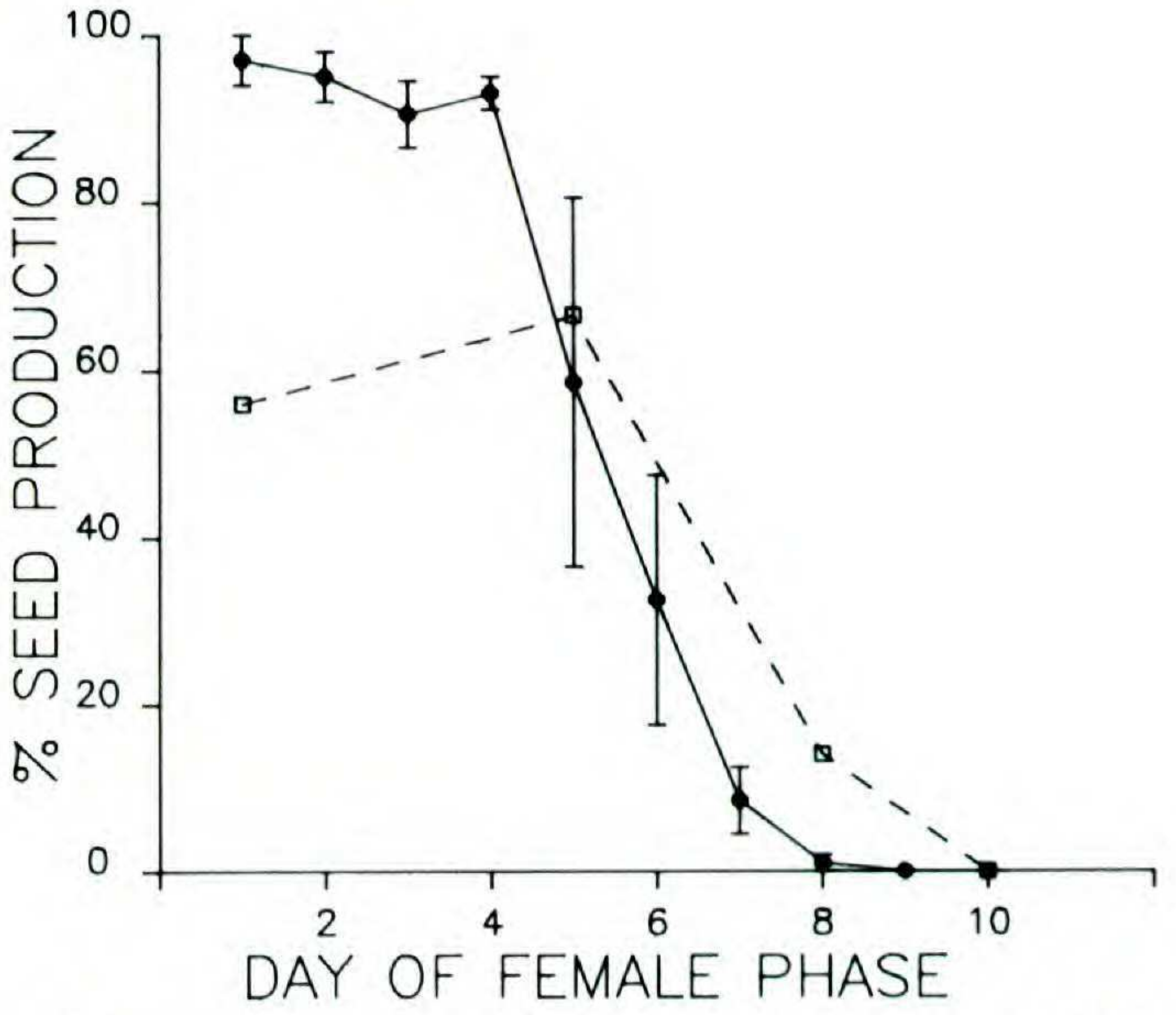


FIGURE 10. Average percentage of ovules producing seed for flowers of *Gentiana saxosa* (solid dots) and *G. serotina* (open squares) following pollination on different days of female phase (mean ± standard error for *G. saxosa*, mean only for *G. serotina*).

same age, but the trend to decreasing reactivity with increasing age was clear in both species (Fig. 9).

In the field, flowers of *G. serotina* reacted similarly to those in the greenhouse. Ten fresh female-phase flowers were all closed on the day following hand pollinations, whereas eight of 10 flowers not pollinated by hand had reopened.

Under fluorescent microscopy, all three stigmas from flowers of *G. serotina* that had been pollinated on the first day of the female phase had numerous germinating pollen grains and many well-formed pollen tubes penetrating the stigma. Of the three stigmas pollinated on their fifth day, two showed good pollen germination and the third had only a few germinating grains. Two of the three stigmas that had not been pollinated until their eighth day had no pollen germinating, and the third had good germination.

The proportion of ovules that developed into good seeds was clearly affected by the age of the stigma when it was pollinated and related well to the responsiveness of flowers to pollination. In both species there was a sharp decrease in seed production for flowers pollinated later than the fourth or fifth days of the female phase (Fig. 10). In *G. saxosa*, flowers pollinated on the first to fourth days of the female phase consistently matured a high proportion of their ovules. Those pollinated on the fifth to seventh days were more variable in seed production, and seed production was related to reactivity of individual flowers. For example, a flower pollinated on the fifth day failed to close and produced no seed, whereas a flower pollinated on the seventh day closed almost completely and had 25% seed production. Few flowers pollinated on the eighth day of the female phase, and none pollinated on the ninth or tenth days produced seed. The pattern of seed production for flowers pollinated at different ages in *G. serotina* was similar (Fig. 10), but the smaller sample size does not allow a detailed analysis.

Thus, although the corolla and stigma may appear fresh for much longer, the functional female phase in both species is only four to eight days. Adding together male and female phases, one gets a reproductively functional flower life of five to 12 days for *G. saxosa*, and six to 14 days for *G. serotina*.

The reaction of flowers that were never pollinated differed between species. In *G. serotina*, the corolla lobes continued to diverge as the flower aged, but eventually began to close (Fig. 7), finally reaching a position similar to that of a late-pollinated flower (Fig. 6) before turning brown after an average of 26 days. However, in *G. saxosa* the corolla lobes reached a strongly recurved position and in all but one of 11 flowers showed no sign of returning to a closed position (Fig. 8) and turned brown after an average of 17 days. In both species some flowers had white, turgid corollas for longer than a month, although the stigmas were dull and blackened by this time and the stamens had altogether withered.

DISCUSSION

Floral longevity of individual flowers may be defined in terms of reproductive function as the period over which a flower is able to receive and/or dispatch pollen. However, outside this period, flowers may perform functions not directly related to their own reproductive success, as in the case of supplemental pollinator attraction provided by late buds and older flowers. Thus, a more practical definition of floral longevity in terms of reproductive success of whole plants may be the period for which a flower is able to attract pollinators. For many plants, particularly tropical species, floral longevity appears to be a predetermined, endogenous characteristic with many such species having 1-day flowers (Dobkin, 1984; Primack, 1985). In some such species, non-induced floral changes, which indicate that the flower is no longer reproductively functional, may occur before full senescence (indicated by abscission or wilting of petals). In others, flowers may be reproductively functional until full senescence (Gori, 1983). The second major pattern is provided by those species in which flower life may be curtailed by pollination (Kerner, 1902; Arditti, 1976; Stead & Moore, 1979; Devlin & Stephenson, 1984). It is important to note that for species in which floral changes are pollination-induced, the potential flower life is still endogenously determined and the pollination-induced changes occur within this outer limit.

Gori (1983) recognized and summarized available data on five basic types of floral change that follow pollination or indicate the end of reproductive function before full senescence: color change, termination of odor and/or nectar production, change in flower orientation, collapse of flower parts, and corolla abscission. To this may be added flower closure as described here for *Gentiana,* and reported by Kerner (1902) for *Mammillaria glochidiata.* In fact, flower closure is likely to be the response in many species in which petals close regularly at night or in dull weather. Although floral changes may prevent or deter pollinator visits, the reproductive, functional end of flower life occurs when no viable pollen is available for dispatch and the stigma ceases to be receptive. In *Gentiana serotina* and *G. saxosa,* the end of reproductive flower life is indicated either by flower closure or the loss of responsiveness of the flower to pollination. Once this occurs, pollen does not germinate on the stigma, and no seeds are produced. The beginning of flower life is marked by the corolla lobes opening to expose the dehisced anthers; all pollen is normally lost before the beginning of the female phase, so pollen availability does not determine the end of flower life, although it may affect flower longevity if the male phase is prolonged by a paucity of pollinator visits as in *Lobelia cardinalis* (Devlin & Stephenson, 1985).

When full senescence of a flower finally occurs, floral changes as listed above may occur. In addition, the whole flower may be aborted, even if pollination has occurred, especially in species that use flower abortion as a means of maternal regulation (Lloyd, 1980; Bawa & Webb, 1984). Within a species, it is possible that the floral changes that occur following pollination may differ from those of flowers that are never pollinated. In both *Gentiana saxosa* and *G. serotina,* fresh female-phase flowers closed in response to pollination; in *G. saxosa,* but not *G. serotina,* the reaction of never-pollinated flowers differed in that flower closure did not occur and petals withered in a recurved position. However, the end of functional pollen and stigma presentation in never-pollinated flowers occurred well before the morphological change of flower closure in *G. serotina* and corolla wilting in *G. saxosa.* The persistence of these flowers well beyond their reproductively functional life may add to the overall floral display of the plant.

Pollination-induced changes in flowers have been interpreted as signals that direct pollinators to unvisited flowers (Allen, 1898; Kerner, 1902; Arditti, 1976; Stead & Moore, 1979; Casper & La Pine, 1984) or help to conceal the developing seeds within pollinated flowers from predators (Allen, 1898), or simply minimize costs of flower maintenance by retaining the perianth no longer than is necessary (Kerner, 1902). Gori (1983) considered three aspects of the first alternative: avoidance of pollinator interference within pollinated flowers, increasing the pollinator's foraging efficiency and so increasing the residence time on the plant, and increasing pollination efficiency by restricting pollinators to receptive (reproductively functional) flowers. In the two species of *Gentiana* studied here, corolla closure clearly signals that the flower is unavailable for visits; in fact it precludes visits, and the corolla also tightly enfolds the developing ovary until it is almost mature, making it less accessible to predators. Field experiments, as described by Gori (1983) for *Lupinus*, would be necessary to determine the precise function of pollination-induced flower closure in *Gentiana*. In many insect-pollinated species, the end of flower life is signalled by corolla abscission and the developing ovary is either inferior or enclosed within infolded bracts or calyx lobes as in *Malvaviscus arboreus* (Webb, 1984b). Corolla closure, rather than abscission, may be necessary to protect the ovary in *Gentiana* because the large superior ovary extends well beyond the small calyx lobes.

In terms of natural selection, flower life for a particular species is likely to be a trade-off between the cost of maintaining the flower in a receptive state and the probability that it has been pollinated. Thus, as originally suggested by Kerner (1902), flower life is likely to be longer for species that normally experience unpredictable weather conditions allowing fewer suitable times for pollinator visits, for species with few, large flowers per plant, and for species that are obligately outcrossing. These suggestions are supported by data on flower life that show that many tropical plants, particularly those flowering in the lowlands during the dry season, have 1-day flowers (Dobkin, 1984; Primack, 1985). Under those conditions pollination is predictable. In contrast, plants of higher altitudes and of temperate areas have long-lived flowers, as might be expected when many days are unsuitable for flower visits. That many large orchid flowers with complex outcrossing mechanisms are long-lived is to be expected because they may have low rates of flower visitation.

There are three strategies that might to some extent ameliorate the difficulty of unpredictable pollination. First, if flower life is pollination-dependent, as in the two species of *Gentiana* described here, then flower maintenance costs are minimized. There is, however, probably a cost in maintaining enzyme systems responsible for pollination-induced floral changes (Gori, 1983). Second, under conditions unfavorable to pollinators, autogamy may occur (Kerner, 1902; Faegri & van der Pijl, 1979); the evolution of autogamy often involves loss of dichogamy or herkogamy, and also a reduction of flower life (Morin, 1983). In some species selfing may be delayed until an opportunity for outcrossing has been provided or may even be a direct response to unfavorable weather conditions. In *Gentiana lineata*, the flowers open fully in warm sunny weather suitable for insect pollination, but on wet or dull days the flowers open only partly so that the anthers dehisce directly onto the stigma (Webb, 1984a); this type of mechanism was termed induced selfing by Schoen and Lloyd (1984). Third, flower life may be much longer during weather unfavorable to pollination, or flowers may open only on suitable days with the floral parts protected during inclement weather (Kerner, 1902).

When floral changes are pollination-induced, flowers are likely to be non-dichogamous or protandrous because flower closure, corolla abscission, and other reactions to pollination, all curtail the time over which pollen can be presented (Lloyd & Webb, 1986). The pollination-induced flower closure described here for *Gentiana* can be effective only if flowers are protandrous; protogyny would preclude pollen presentation, and adichogamy would severely limit the male phase.

Flower life may appear to be the simple result of proximate causes—especially of weather conditions and pollinator availability. However, the average flower life for a population, the particular response of flowers to pollination, and the cues used to determine the time of senescence, must all be the result of natural selection. Yet, the selection of these factors has seldom received the attention of reproductive biologists in spite of the important part they play in determining the success of plants as pollen or seed parents.

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